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A LABORATORY STUDY OF GERMAN COCKROACH DISPERSAL (DICTYOPTERA: BLATTELLIDAE)

BRIAN L. BRET AND MARY H. ROSS

Department of Entomology, Virginia Polytechnic Institute & State University, Blacksburg, Virginia 24061.

Abstract.—Dispersal of German cockroaches within a system of interconnected aquaria was studied. Mixed age groups of two strains were released in one aquarium and held sufficiently long for aggregate groups to form within shelters that were provided, along with water and food. Subsequently, access to a second and third aquarium was opened. The second (middle) one was empty; the more distant was provided with water, shelter, and food. Distribution of each age class was recorded at the end of one week. Each class was divided equally between the two strains, but the data were pooled since no strain difference was evident. A second experiment was conducted that determined whether a loss of early instars in the first experiment was due to immediate escape rather than movement away from an aggregate group. The combined results of the two experiments showed that least movement from aggregations that formed in the first aquarium was by early instars and most movement by middle instars. Adult movement was intermediate. Movement of females and middle instars decreased significantly when female density in mixed age groups was increased.

The German cockroach, *Blattella germanica* (L.), has been the subject of many biological studies (Cornwell, 1968; Guthrie and Tindall, 1968). Nevertheless, there is little information available on dispersal of adults and nymphs. Movement within and between apartments was reported by Akers and Robinson (1981) and Owens and Bennett (1982), but these studies were either limited to observations on adults or life stage was unaccounted for. The latter found adult movement to be more prevalent where apartments shared plumbing. Whether such information is a reliable guide to the proportion of a population moving from one harborage to another depends on whether other members of the population show similar rates and amounts of dispersal. A laboratory study showed marked differences occurred in within-harborage aggregation according to age class and sex and to female density and reproductive state (Bret et al., 1983). The results left little doubt that these varying behaviors stemmed from communicatory activities, presumably involving pheromones. Dispersal might also be affected by these factors.

The research presented here describes the results of a laboratory study of movement of adults and nymphs of *B. germanica*. The objectives were to determine whether and in what manner movement from an established group (aggregation) varied according to age class and adult sex, and whether these patterns were affected by the density of adult females.

Materials and Methods

Three 32 cm × 22 cm × 21 cm glass aquaria were used for each experiment with mixed age groups. Two ends were replaced with plexiglass that had 3.2 cm diameter holes centered 2.5 cm from the bottom. The aquaria were connected linearly by Tygon® tubing (30.5 cm long; diam. 3.2 cm). This was wider than spaces favored for aggregation (Berthold and Wilson, 1967) so that cockroaches would use the tubes for movement but not harborage. The inside walls of the aquaria were coated with a film of petroleum jelly, and lids were placed on each aquarium to limit escape. The aquaria were numbered 1, 2, and 3. Aquaria 1 and 3 were provided with four 1.0 cm × 4.0 cm × 10.0 cm shelters made out of black construction paper. Aquarium 2 was left empty. Dog food pellets and water containers were placed near the shelters in Aquaria 1 and 3 in order to minimize movement related to search for water and food (foraging). Aquaria and tubing were washed thoroughly with detergent and rinsed several times before reusing.

Groups of cockroaches were released in Aquarium 1. It was sealed off from the other aquaria. The cockroaches were allowed to acclimate to their surroundings for 2 days. A prior study using the same materials as in the first aquarium showed that the majority of the population aggregated in the shelters within 2 days (Bret et al., 1983). At the end of the 2nd day, the connections between the aquaria were opened. One week later, each aquarium was sealed and censused.

Cockroaches were drawn from two strains, the VPI strain and a black-body mutant (*Bl*) strain. The VPI strain is a wild-type strain that has been in culture for approximately 40 years, and thus has never been exposed to insecticides. It is used frequently in toxicological and genetic studies. The *Bl* cockroaches were homozygotes selected from the F_2 of crosses between the original *Bl* strain and a freshly-collected field strain. The black-body mutant was isolated following irradiation of a strain collected in Alabama in 1959 (Ross and Cochran, 1966).

Each group consisted of 4, 8, or 16 adult females; 4 adult males; 16 middle instars (3rd–4th stadium); and 16 early instars (1st–2nd stadium). They were equally divided between VPI and *Bl* cockroaches. Individuals of each instar group tested were known to have hatched within the same weekly period. This synchronization was sufficient to insure two readily separable nymphal age classes at the end of one week. Late instars were not used because they might mature and thus be inseparable from the adults. Adults were from a breeder jar in which the oldest individuals were less than 2 months old. Adult females either carried oothecae at the start of the experiment or, if not, most formed oothecae prior to censusing. Experiments using 4 and 8 females were replicated 12 times; those with 16 females had 14 replicates.

A major problem occurred in the above experiments due to escape of early instars (>50%). It could not be determined whether this represented movement before or after they had settled into aggregate groups (a behavior typical of cockroaches). A 2nd experiment using early instars only (VPI strain) was conducted in order to resolve this problem. Since the results from the two strains in the first experiment were nearly identical (117 VPI vs. 118 *Bl* early instars in aquarium 1 at the end of one week), we used only the single strain in the 2nd experiment. Two rather than 3 inter-connected aquaria were used. Each was supplied with water, food, and shelter, similar to Aquaria 1 and 3 in the mixed age group experiments. Sixteen early instars were released and held in Aquarium 1. The

Table 1. Comparison between the numbers of wild-type and black-body cockroaches present in Aquarium 1 after one week.

Female Density	Number and Phenotype in Aquarium 1[a]									
	♀		♂		M		E		Total[c]	
	+	*Bl*	+	*Bl*	+	*Bl*	+	*Bl*	+	*Bl*
4	12	10	17	17	37	30	38	39	104	96
8	31	27	18	16	48	42	43	46[b]	140	131
16	93	95	25	25	75	76	36	33	229	229
Total[c]	136	132	60	58	160	148	117	118	473	456

[a] +—wild-type (VPI strain); *Bl*—black-body; ♀—adult females; ♂—adult males; M—middle instars; E—early instars.

[b] One early instar not included in calculations. Recent molt prevented classification as + or *Bl*.

[c] Numbers of wild-type and black-body have good fits to 1:1 ratios (χ^2 <0.50, and >0.40 for each female density and each age/sex class).

number remaining at 24 h post-release was counted. Access to Aquarium 2 was opened. The numbers present at 24 h and at 7 d post-opening were recorded. The experiment was replicated 11 times.

Dispersal of mixed age groups was measured using the following index: $DI = (X - Y)/X$, where X = number of cockroaches in the first aquarium at the beginning of the experiment, Y = number of cockroaches remaining the first aquarium after one wk, and $(X - Y)$ = number of cockroaches dispersed from the first aquarium in one week. The dispersal index ranges from 0 (no dispersal) to 1 (complete dispersal). The higher the index the greater the dispersal. Comparisons of the three densities were tested using the Kruskal-Wallace non-parametric n-way comparisons test. An alpha level less than 0.05 was used to determine significance.

Results

Table 1 shows the results of the mixed age group experiment separated according to black-body (*Bl*) and wild-type individuals. The numbers of each strain that remained in Aquarium 1 at the end of one week were not significantly different. This was apparent in comparisons between each age/sex class at each of the three female densities. Since no strain difference in movement away from Aquarium 1 was found, the following analyses of dispersal are based on the pooled data from the mixed age groups (Tables 2 and 4).

Table 2 shows the results of the experiments using mixed age groups. Cockroaches that remained in the system of inter-connected aquaria had sufficient time for formation of within-shelter aggregations (Bret et al., 1983). Since relatively few adults and middle instars escaped from the system, it is assumed that those not in Aquarium 1 at the end of one week had moved away from aggregate groups that had formed in this aquarium. A similar assumption could not be made for early instars since over half of them had escaped. Therefore, the results pertaining to early instars are presented separately from the other age/sex classes, using data from both the mixed age class experiments and those designed to test the time of escape of early instars (Table 3).

Over 80% of the adults and middle instars were in the aquaria supplied with water, food, and shelter at the end of one week (Table 2, Aquaria 1 and 3). The

Table 2. Distribution of German cockroaches throughout a system of inter-connected aquaria one week after opening tubes that allowed movement out of Aquarium 1.

Age-Sex Class[a]	Observation[b]	Aquarium 1	Aquarium 2	Aquarium 3	Tubes	Escaped
♀	n	268	17	49	28	8
	$\bar{x} \pm$ SE	7.05 ± 2.18	0.45 ± 1.99	1.29 ± 1.32	0.74 ± 1.89	0.21 ± 1.45
	%	72.4%	4.6%	13.2%	7.6%	2.2%
♂	n	118	4	30	6	3
	$\bar{x} \pm$ SE	3.10 ± 0.62	0.10 ± 1.20	0.79 ± 0.98	0.16 ± 0.93	0.08 ± 0.97
	%	73.3%	2.5%	18.6%	0.7%	1.9%
M	n	308	32	145	41	71
	$\bar{x} \pm$ SE	8.10 ± 1.67	0.38 ± 1.67	3.82 ± 1.59	1.08 ± 1.88	1.89 ± 1.31
	%	51.6%	5.4%	24.3%	6.9%	11.9%
E	n	236	6	28	4	334
	$\bar{x} \pm$ SE	6.21 ± 1.59	0.16 ± 1.38	0.74 ± 1.57	0.10 ± 1.20	8.76 ± 1.42
	%	38.8%	1.0%	4.6%	0.7%	54.9%
	%[c]	86.1%	2.2%	10.2%	1.5%	—

[a] Symbols: see Table 1.

[b] Categories: n—total of all replications (no. of middle instars 11 less than released; that of adult males increased by 9 and females by 2); $\bar{x} \pm$ SE—mean and standard error from 38 replicates. %—relative proportions within each location (based on n).

[c] Distribution of early instars that remained within the experimental system.

largest proportion of each of these classes was still in Aquarium 1, but differences occurred in the relative proportions of those that had moved to other parts of the system. Middle instars dispersed more than either adult males or females; dispersal of males resembled that of females (but see results at differing female densities). The distribution of these classes in Aquarium 3 differed from that in the parent group in Aquarium 1. In Aquarium 1, the distribution was as follows: 38.6% females, 17.0% males, and 44.4% middle instars; that in Aquarium 3, 21.9% females, 13.4% males, and 64.7% middle instars.

The experiments using only early instars showed that most escapes from the experimental system occurred before the connection to Aquarium 2 was opened (Table 3). Subsequently, distribution stabilized. Little change occurred between the 1st and 7th day post-access to Aquarium 2. The total loss from Aquarium 1 represented 44.3% as compared to 54.9% in the mixed age group experiments. In the former, 40.3% was due to escape within the first 24 h. This left 112 early instars within the system, of which 98 (87.5%) were in Aquarium 1 at the end of one week. Among 274 early instars that remained in the system in the mixed age group experiments, 236 (86.1%) were in Aquarium 1.

Table 4 shows the effect of increased female density on dispersal in experiments with mixed age groups. A clear trend towards decreased dispersal with increased density occurred among the adult females, males, and middle instars. Males dispersed less than females and middle instars and responded less to changes in female density. A significant change occurred among the females and middle instars between the lowest and highest female densities. As noted above, it is reasonably certain that movement of adults and middle instars was away from groups established in Aquarium 1, in contrast to that of early instars. The ex-

Table 3. Distribution of early instars prior to and after opening tubes between Aquarium 1 and 2 in experiments using only early instars.

	First 24 h		24 h Post-opening			7 Days Post-opening		
Observation[a]	Aquarium 1	Escape	Aquarium 1	Aquarium 2	Escape	Aquarium 1	Aquarium 2	Escape
n	111	65	105	5	1	98	7	5
$\bar{x} \pm$ SE	10.2 ± 2.0	5.8 ± 2.7	9.5 ± 2.1	0.45 ± 0.77	0.9 ± 0.9	8.9 ± 2.1	0.64 ± 0.84	0.45 ± 1.22
%	62.5%	36.9%	59.7%	2.8%	0.6%	55.7%	4.0%	2.8%

[a] Like Table 2 except that the experiment was replicated 11 times; percent is based on the total released (176).

Table 4. The effect of female density on dispersal of mixed age groups out of Aquarium 1.

Female Density	Dispersal Index for Each Age/Sex Class[a] ♀	♂	M	E[b]
4	0.54	0.29	0.65	0.12
8	0.40	0.30	0.53	0.11
16	0.17[c]	0.11	0.33[c]	0.16

[a] Age/sex class as in Table 1. Dispersal index = difference between the no. of cockroaches released in Aquarium 1 and those present at the end of the experiment (1 wk) divided by the number released in Aquarium 1 (0 = no dispersal; 1 = complete dispersal).

[b] Calculated from nos. that remained in the experimental system (see text for explanation).

[c] Significant difference ($P < 0.05$) between lowest and highest female density (Kruskal-Wallace non-parametric n-way comparison).

periments on early instars (Table 3) provided strong evidence that the heavy loss of early instars in mixed age group experiments occurred soon after release rather than from an aggregate group. Therefore, the dispersal indices for early instars in Table 4 are based on the most nearly comparable data to that of the other classes, i.e., early instars known to have remained in the system. Little dispersal of early instars occurred among those that remained in the system and there was no decrease with increased female density.

Discussion

Three sources are generally recognized as being of fundamental importance to cockroach distribution—food, water, and harborage (concealment). They were available to mixed age groups only in the first and third aquaria. It is hardly surprising that most of the cockroaches were in these locations at the end of the experiment.

The movement studied in our experiments is alluded to as "dispersal" rather than foraging. Food and water were supplied close to the shelters in which the cockroaches aggregated in Aquarium 1, thereby negating the need to forage. Cockroaches that found these resources in Aquarium 3 left an aggregation, discovered and moved through openings into the middle aquarium, and also traversed this aquarium. This behavior seems to us more consistent with a dispersal behavior than a search for water or food.

The comparatively high dispersal of middle instars and low dispersal of early instars from groups formed in Aquarium 1 agrees well with expectations based on studies that have implicated the aggregation pheromone. Early instars have a particularly strong response to the pheromone (Pettit, 1940; Ledoux, 1945; Ishii and Kuwahara, 1967). They clustered more intensely within shelters in experiments on within-shelter aggregation than other age classes (Bret et al., 1983). Sommer (1975b) noted that a tendency of nymphs to be absent from hiding places increased with age. He suggested that older nymphs are less responsive to the aggregation pheromone. That seems to be the most likely explanation of the results reported here. We do not know whether initial escape of early instars reflected a slow response to aggregation pheromone and/or other signals by insects that had found concealment, the lack of adequate thigmotaxic stimulation (Berthold and Wilson, 1967), or simply the fact their small size could have facilitated escape from under the lid of the aquarium before there was sufficient time for formation of an aggregation. The greater movement of middle instars was responsible for their forming a larger proportion of the newly-formed group in Aquarium 3 than in their parent group. If this has an application to field situations, infestations in which middle to late stage nymphs predominate could be indicators of newly established populations. The present data support the idea that a recent infestation accounted for predominance of mid–late instars in a collection from an apartment (Sherron et al., 1981).

The data showing adult males dispersed less than either females or middle instars are more difficult to reconcile with the results of other studies. Sommer (1975a) reported adult males were the most active component of a population; Owens and Bennett (1982) found adult males more mobile than females in inter- and intra-apartment movement; Bret et al. (1983) found males showed less aggregation within shelters than any other member of the population, except where populations contained only four non-egg case bearing females and four males. One possibility is that the present experiments differed because movement was away from a nearby source of water and food, whereas a search for these resources may have been involved in experiments reporting greater male movements.

Dispersal, like within-harborage aggregation (Bret et al., 1983), was affected by female density. Within-harborage aggregation increased with increased density of egg case carrying females; dispersal of the experimental groups decreased with similar changes in female density. These behaviors can almost certainly be attributed to increased levels of aggregation pheromone associated with increased numbers of females. Predominance of egg case carrying females in the dispersal experiment probably contributed to the similarity. Among individual age/sex classes, early instars were unique in that dispersal remained low at all female densities. The amount of aggregation pheromone associated with the group in Aquarium 1 at the lowest female density was probably sufficient to exert a maximal attraction. A significant decrease in dispersal at highest female density occurred among both adult females and middle instars, but the magnitude of the decrease was less among the latter. The stronger tendency of middle instars than of other age/sex classes to disperse from the larger groups heightened the disparity between their dispersal behavior and that of other components of the experimental populations. Apparently aggregation pheromone and/or other factors associated with increased female density had a greater effect on adult females and also the males than on middle instars. Possibly middle instars are "colonizers" that disperse regardless of group size. In contrast, dispersal behavior of other age/sex classes might be affected by greater sensitivity to varying levels of aggregation pheromones, sex pheromones, or particular environmental situations such as crowding or food availability.

Deleterious changes in mating ability and other behaviors often occur when insects are transferred from the field to laboratory culture. However, transference of German cockroaches to a laboratory places them in a fairly optimal environment. Wright (1967) found that laboratory rearing increased the fecundity in a "field" strain. Therefore, it is not entirely surprising that we found no difference in dispersal between the long-time laboratory strain and the black-body strain that had been crossed to a freshly-collected "field" strain.

A second explanation of the absence of a strain difference in dispersal should also be considered. The observed behaviors may be typical of the species and thus unlikely to differ with strain. Innate, stereotyped behavioral patterns exist in animals—behaviors that have been shaped by evolution and that characterize the species (Scheller and Axel, 1984). The results of the present experiments are reminiscent of advantageous adaptive strategies of flying insects that involve dispersal before egg development and "while flight system is maximized and that of the reproductive system minimized" (Mathews and Mathews, 1978). Greatest dispersal of German cockroaches was by an age class, i.e., middle instars, that is almost certainly less susceptible to mortality than 1st–2nd instars but that has a near maximal time for movement before maturation and egg case formation by the females. Conceivably, the decrease in dispersal of all age classes with increased densities is also an adaptive strategy. It could decrease movement away from favorable situations where the available resources had encouraged development of a large group and egg case formation by the females.

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